CHROMOSOME NUMBERS IN COMPOSITAE. XIII. EUPATORIEAE[1]

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ABSTRACT

New chromosome counts are provided for 234 populations of the tribe Eupatorieae including the first reports for the genera: *Asplundianthus, Carminatia, Cronquistia, Decachaeta, Guevaria, Heterocondylus, Matudina, Peteravenia, Phalacraea, and Sclerolepis.* Chromosome data is summarized on the basis of over 325 of about 2,000 species in the tribe representing 70 of the 160 known genera. Cytology is correlated with recent taxonomic revisions including new generic concepts and reidentification of many vouchers of previous cytological studies. The number $n = 10$ is regarded as basic for the tribe; it is the most common in the tribe and is characteristic of most groups of genera. Important derivatives include specialized members of the *Brickellia* series with $x = 9$ and members of the *Piqueria, Stevia, Carphochaete, Microspermum* series with $x = 11$ and 12. The *Bartlettina* series has a base of $x = 16$ but is closely related to *Hebeclinium* with $x = 10$. Other groups with higher numbers are more distinctive, *Neomirandea* subgenus *Critoniopsis* with $x = 17$, subgenus *Neomirandea* with $x =$ ca. 20 and ca. 25, *Mikania* with $x = 16–20$, *Ageratina* with mostly $x = 17$, *Oxylobus* with $x = 16$. *Hofmeisteria* with $x = 18–19$ is regarded on other bases as one of the most distinctive elements in the tribe. Individual examples of reduction in groups with a base of $x = 10$ are *Adenostemma involucratum* with $n = 5$ and the weedy *Fleischmannia microstemon* with $n = 4$.

The present paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974) and is the first devoted to the tribe Eupatorieae. Included here is a summary of previous studies and combined reports of some of the present authors. An attempt is made to correlate results with the extensive systematic revisions of two of the authors (King, 1967a, 1967b; King & Robinson, 1967, 1969–1975b).

Unless otherwise indicated the chromosome counts have been made from acetocarmine or aceto-orceine squashes of microsporocytes in meiosis. Voucher specimens are available for all counts. Vouchers for the King collections are in the U.S. National Herbarium (US) and a nearly complete set is at the Missouri Botanical Garden (MO). Vouchers for other collections are deposited in the Dudley Herbarium (DS), Stanford University, unless otherwise indicated. In Table 1 those collection numbers preceded by *B* are by Breedlove, by *K* are by King, and by *R* are by Raven.

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Of the approximately 2,000 species of the Eupatorieae, chromosome numbers are known for 327 species. These include members of 70 of the 160 known genera. Nine genera, *Asplundianthus*, *Carminatia*, *Cronquistia*, *Decachaeta*, *Guevaria*, *Heterocondylus*, *Matudina*, *Peteravenia*, *Phalacraea*, and *Sclerolepis*, are newly reported in this paper. The 56 species reported here for the first time are marked by an asterisk in Table 1.

Evaluation of previous reports has required reorganization of data into new tribal and generic concepts based largely on details of floral anatomy. The tribe Eupatorieae is interpreted here to include *Isocarpha* and *Lepidesmia* which are sometimes placed in the Heliantheae (King & Robinson, 1970f), and *Microspermum* and *Iltisia* which are sometimes placed in the Helenieae (Rzedowski, 1970). Excluded are *Adenostyles*, now placed in the Senecioneae (Toman et al., 1968) and *Dyscritothamnus* which is a member of the Heliantheae.

Revisions at the generic level have provided the most significant basis for interpreting cytological data. The most striking example is the dissection of the older concept of *Eupatorium*, a genus which had over 900 species. These species had a meaningless series of chromosome numbers, including $n = 4$, 8, 10, 11, 12, 15, 17, 18, 20, 25 and multiples. One other species falling within the old concept had been counted at $n = 9$, but was removed to *Brickellia* on the basis of this chromosome number (Harcombe & Beaman, 1967). Other generic concepts have been altered to a lesser extent. The chromosome numbers credited to *Alomia* belong to species that have been transferred to *Ageratum*. In *Piqueria*, chromosome counts of $n = 10$, 12, 24, and 25 have been reported, but the determination of $n = 10$ is from a South American species now placed in the genus *Ophryosporus*.

Many previous reports have been based on misidentified material and some of these represent generic differences. Reports for what is generally called *Eupatorium ballotifolium* H.B.K. (Coleman, 1968, 1970) are not of that species but of *Conocliniopsis prasiifolia* (DC.) K. & R. The true *E. ballotifolium* is a *Lourteigia* and has been reported as *Eupatorium* aff. *pycnocephaloides* (Powell & King, 1969). The latter species is a *Fleischmannia* and is reported for the first time in this paper. Chromosome counts reported for *Trichogonia gardneri* Gray should be treated under the name *Trichogoniopsis adenantha* (DC.) K. & R. Asa Gray had erroneously considered the two species as distinct. Material in most herbaria under the name *E. adenanthum* actually belongs to the distinct genus *Macropodina*. A report of $n = 10$ has been credited to *Eupatorium* cf. *ligustrinum* (Turner et al., 1961) which is a member of the genus *Ageratina*, a genus which has a basic chromosome number of $x = 17$. The voucher has been seen and proves to be *Koanophyllon albicaule* (Sch.-Bip. ex Klatt) K. & R. Some additional corrections of identification within genera are mentioned below, with notable examples in *Adenostemma* and *Fleischmannia*.

General Considerations

Gaiser (1954) observed that chromosome numbers lower than $n = 9$ did not occur in the *Eupatorieae*. Since that time the gametic chromosome number $n = 4$ has been discovered in two species of *Fleischmannia*, a number of $n = 5$ has

TABLE 1. Chromosome counts, localities and vouchers for species of Eupatorieae.

Species	*n*	Locality and collection number
Adenostemma platyphyllum Cass.	10	ECUADOR. EL ORO: ca. 30 kms NE of Machala, *K6934*.
Adenostemma platyphyllum	10	ECUADOR. CHIMBORAZO: 35 kms NE of El Triunfo, *K6955*.
Adenostemma platyphyllum	10	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6869*.
Ageratina altissima (L.) K. & R.	ca. 17	UNITED STATES. NORTH CAROLINA: Haywood Co., *R20479*.
Ageratina altissima	ca. 17	UNITED STATES. INDIANA: Monroe Co., *R20499*.
Ageratina anisochroma (Klatt) K. & R.	ca. 17	COSTA RICA. SAN JOSÉ: ca. 17 kms NW of Empalme, *K6411*.
Ageratina anisochroma	17	COSTA RICA. ALAJUELA: Volcán Poás, *K6428*.
Ageratina anisochroma	17	COSTA RICA. SAN JOSÉ: La Palma, *K6740*.
Ageratina anisochroma	ca. 17	COSTA RICA. SAN JOSÉ: La Palma, *K6741*.
Ageratina anisochroma	17	COSTA RICA. CARTAGO: ca. 9 kms NE of San Rafael de Irazú, *K6836*.
Ageratina aschenborniana (Schauer) K. & R.	17	MEXICO. CHIAPAS: Mun. Puebla Nuevo Solistahuacán, *R19926*.
Ageratina aschenborniana	ca. 20	COSTA RICA. SAN JOSÉ: ca. 25 kms S of Cartago, *K6755*.
Ageratina aschenborniana	ca. 17	COSTA RICA. CARTAGO: El Muñeco, *K6770*.
Ageratina aschenborniana	17	COSTA RICA. SAN JOSÉ: ca. 3 kms N of El Copey, *K6789*.
Ageratina aschenborniana	17	COSTA RICA. CARTAGO: 2 kms NE of Santa Rosa, *K6814*.
Ageratina aschenborniana	ca. 17	COSTA RICA. CARTAGO: ca. 3 kms S of Pacayas, *K6830*.
Ageratina aschenborniana	ca. 84_{I} (2 cells ca. $160–166_{I}$)	GUATEMALA. SAN MARCOS: 6 kms NW of Palestina, *K7035*.
Ageratina aschenborniana	ca. 10	GUATEMALA. TOTONICAPÁN: 49 kms ESE of San Cristóbal Totonicapán, *K7061*.
**Ageratina azangaroensis* (Sch.-Bip. ex Wedd.) K. & R.	17	ECUADOR. COTOPAXI: ca. 27 kms S of Aloag, *K6519*.
Ageratina azangaroensis	17_{II} + 1 frag.	ECUADOR. TUNGURAHUA: 1 km SE of Ambato, *K6532*.
Ageratina azangaroensis	17	ECUADOR. CHIMBORAZO: ca. 6 kms S of Mocha, *K6580*.
Ageratina azangaroensis	17	ECUADOR. BOLÍVAR: ca. 22 kms NE of Guaranda, *K6593*.
Ageratina azangaroensis	17_{II} + 1 frag.	ECUADOR. AZUAY: ca. 22 kms W of Cuenca, *K6667*.
Ageratina azangaroensis	17_{II} + 21 or round frag.	ECUADOR. CHIMBORAZO: 45 kms SW of Riobamba, *K6974*.
**Ageratina barbensis* K. & R.	17	COSTA RICA. HEREDIA: ca. 22 kms N of Barba, *K6409*.
**Ageratina bellidifolia* (Benth.) K. & R.	68–69	MEXICO. CHIAPAS: Mun. Chamula, *B8005*.
**Ageratina chiapensis* (B. L. Rob.) K. & R.	ca. 16	MEXICO. CHIAPAS: Mun. Chamula, *B6670*.
Ageratina chiapensis	17	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9054*.

TABLE 1. (Continued).

Species	n	Locality and collection number
*_Ageratina conspicua_ (Kunth & Bouche) K. & R.	ca. 25	MEXICO. CHIAPAS: Mun. Chamula, _B9800._
*_Ageratina costaricensis_ K. & R.	70–100$_{\mathrm{I}}$	COSTA RICA. CARTAGO: ca. 1 km NE of San Rafael de Irazú, _K6816._
*_Ageratina exerto-venosa_ (Klatt) K. & R.	ca. 42	ECUADOR. AZUAY: ca. 17 kms E of Gualacéo, _K6632._
Ageratina exerto-venosa	ca. 40 + B chromosomes	ECUADOR. AZUAY: 32 kms S of Cumbe, _K6899._
Ageratina exerto-venosa	ca. 40 + B chromosomes	ECUADOR. LOJA: 2 kms E of Loja, _K6914._
Ageratina exerto-venosa	ca. 40	ECUADOR. LOJA: 2 kms E of Loja, _K6915._
Ageratina cf. _glechonophylla_ (Less.) K. & R.	17_{II} + 2 frags.	ECUADOR. BOLIVAR: ca. 28 kms SW of Ambato, _K6587._
*_Ageratina ixioclada_ (Benth. ex Oerst.) K. & R.	17	COSTA RICA. CARTAGO: 3 kms NE of San Rafael de Irazú, _K6818._
*_Ageratina ligustrina_ (DC.) K. & R.	17	MEXICO. CHIAPAS: Mun. Tenejapa, _B6805._
Ageratina ligustrina	ca. 50	MEXICO. CHIAPAS: Mun. Chamula, _B7797._
Ageratina ligustrina	55	MEXICO. HIDALGO: Zimapán (progeny) _R13777, R13830._
*_Ageratina mairetiana_ (DC.) K. & R.	17	MEXICO. CHIAPAS: Mun. Zinacantán, _B9505._
Ageratina mairetiana	17	MEXICO. OAXACA: Monte Alban, _K6462._
Ageratina petiolaris (DC.) K. & R.	17	MEXICO. CHIAPAS: San Cristóbal las Casas, _R20062._
*_Ageratina pichinchensis_ (H.B.K.) K. & R.	30–34	ECUADOR. CAÑAR: ca. 14 kms NW of Azogues, _K6616._
Ageratina pichinchensis	33 ± 2	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, _K6656._
Ageratina pichinchensis	ca. 30	ECUADOR. CHIMBORAZO: 20 kms SW of Riobamba, _K6964._
Ageratina aff. _pringlei_ (B. L. Rob. & Greenm.) K. & R.	17	MEXICO. CHIAPAS: Mun. Zinacantán, _B7987._
*_Ageratina pseudochilca_ (Benth.) K. & R.	ca. 42	ECUADOR. AZUAY: 17 kms S of Cumbe, _K6891._
*_Ageratina subcordata_ (Benth. ex Oerst.) K. & R.	17	COSTA RICA. SAN JOSÉ: ca. 18 kms SW of Empalme, _K6412._
Ageratina sp.	17	MEXICO. CHIAPAS: Mun. Chamula, _B6725._
Ageratina sp.	17	MEXICO. CHIAPAS: Mun. La Trinitaria, _B9741._
Ageratum houstonianum Mill.	20	ECUADOR. TUNGURAHUA: ca. 7 kms E of Baños, _K6543._
Ageratum houstonianum	10	MEXICO. CHIAPAS: Mun. Las Margaritas, _B9135._
Ageratum nelsonii (B. L. Rob.) M. F. Johnson	ca. 10	MEXICO. CHIAPAS: Tapanatepec, _B13722._
Ageratum rugosum Coult.	10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, _B13892._
*_Aristeguietia buddleaefolia_ (Benth.) K. & R.	10	ECUADOR. AZUAY: ca. 12 kms N of Gualacéo, _K6626._
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 10 kms SE of Gualacéo, _K6628._
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 16 kms N of Sigsig, _K6645._
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 7 kms S of Paute, _K6692._

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: 6 kms SE of Cumbe, *K6692*.
Aristeguietia buddleaefolia	10 or 11	ECUADOR. AZUAY: 5–6 kms NE of Cuenca, *K6873*.
Aristeguietia buddleaefolia	ca. 10	ECUADOR. AZUAY: 10 kms SE of Cumbe, *K6887*.
Aristeguietia buddleaefolia	ca. 10	ECUADOR. AZUAY: 12 kms SE of Cumbe, *K6889*.
**Aristeguietia dielsii* (B. L. Rob.) K. & R.	10	ECUADOR. TUNGURAHUA: 48 kms NE of Guranda, *K6984*.
**Aristeguietia glutinosa* (H.B.K.) K. & R.	10	ECUADOR. CHIMBORAZO: ca. 16 kms W of San Juan, *K6603*.
**Asplundianthus pseudoglomeratus* (Hieron.) K. & R.	ca. 10	ECUADOR. PICHINCHA: ca. 3 kms SW of Chillogallo, *K6510*.
Asplundianthus pseudoglomeratus	10	ECUADOR. PICHINCHA: ca. 10 kms W of Quito, *K6732*.
Austroeupatorium inulaefolium (H.B.K.) K. & R.	10	ECUADOR. TUNGURAHUA: ca. 11 kms E of Baños, *K6547*.
Austroeupatorium inulaefolium	10	ECUADOR. LOJA: 4 kms E of Loja, *K6917*.
**Ayapana ecuadorensis* K. & R.	10	ECUADOR. CAÑAR: 24 kms ESE of El Triunfo, *K7000*.
Ayapana ecuadorensis	10	ECUADOR. CAÑAR: 77 kms ESE of Guayaquil, *K6872*.
**Bartlettina breedlovei* K. & R.	16	GUATEMALA. Mun. San Mateo Ixtatán, *B8717*.
Bartlettina breedlovei	16	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9075*.
**Bartlettina guatemalensis* K. & R.	16	GUATEMALA. Mun. San Mateo Ixtatán, *B8718*.
Bartlettina sordida (Less.) K. & R.	16	MEXICO. CHIAPAS: Mun. Tenejapa, *B9408*.
**Bartlettina tuerckheimii* (Klatt) K. & R.	16	MEXICO. CHIAPAS: Mun. Jitotal, *R19794*.
Brickellia adenocarpa B. L. Rob. var. *glandulipes* B. L. Rob.	ca. 9	MEXICO. CHIAPAS: Mun. Teopisca, *R20067*.
**Brickellia arguta* B. L. Rob.	9	UNITED STATES. NEW MEXICO: Nye Co., *R18931*.
Brickellia argyrolepis B. L. Rob.	9	COSTA RICA. ALAJUELA: 2 kms SW of Zarcero, *K6431*.
**Brickellia atractyloides* A. Gray	9	UNITED STATES. ARIZONA: Mohave Co., *R17366*.
Brickellia californica T. & G.	9	UNITED STATES. CALIFORNIA: Los Angeles Co., *R11350*.
**Brickellia guatemalensis* B. L. Rob.	9	MEXICO. CHIAPAS: Mun. Chamula, *B8014*.
Brickellia guatemalensis	9	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8081*.
Brickellia guatemalensis	9	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *R20063*.
Brickellia incana A. Gray	$2n = 27$	UNITED STATES. CALIFORNIA: San Bernardino Co., *R15494*.
**Brickellia leptophylla* (Scheele) Shinners	9	MEXICO. DURANGO: Ciudad Durango, *B15507*.
Brickellia schaffneri (A. Gray) Shinners	9	MEXICO. JALISCO: San Juan del Río, *B15460*.
Brickellia veronicifolia (H.B.K.) A. Gray	9	MEXICO. PUEBLA: Tehuacán, *B14191*.
**Carminatia tenuifolia* DC.	10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, *B13346*.
**Chromolaena collina* (DC.) K. & R.	10	MEXICO. CHIAPAS: Tapanatepec, *B8837*.
Chromolaena laevigata (Lam.) K. & R.	ca. 20	ECUADOR. LOJA: ca. 27 kms W of Chinchas, *K6929*.
Chromolaena laevigata	ca. 20	ECUADOR. TUNGURAHUA: E of Baños, *K6987*.

TABLE 1. (Continued).

Species	n	Locality and collection number
Chromolaena odorata (L.) K. & R.	30	MEXICO. SINALOA: Concordia (progeny), *B1596*.
Chromolaena odorata	ca. 31 + 41	MEXICO. CHIAPAS: Mun. Bochil, *B8837*.
Chromolaena odorata	60_{I}	MEXICO. CHIAPAS: Mun. Tenejapa, *B9430*.
**Chromolaena opadoclina* (Blake) K. & R.	10	MEXICO. CHIAPAS: Mun. Jitotal, *R19935*.
Chromolaena sagittata (A. Gray) K. & R.	20	MEXICO. SINALOA: Río de Presidoa (progeny), *B1580*.
Condylidium iresinoides (H.B.K.) K. & R.	10	ECUADOR. GUAYAS: 33 kms NE of El Triunfo, *K6951*.
Conoclinium coelestinum (L.) DC.	10	UNITED STATES. LOUISIANA: Bossier Parish, *R20391*.
**Critonia hospitalis* (B. L. Rob.) K. & R.	ca. 10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, *B13869*.
Critonia morifolia (Miller) K. & R.	10	GUATEMALA. SACATEPEQUEZ: Ciudad Vieja, *K7077*.
Critonia morifolia	10	GUATEMALA. GUATEMALA: 20 kms E Villa Canales, *K7083*.
**Critonia sexangularis* (Klatt) K. & R.	10	MEXICO. CHIAPAS: Mun. Pueblo Nuevo Solistahuacán, *R20010*.
**Cronquistia pringlei* (S. Watson) R. M. King	12	MEXICO. DURANGO: Ciudad Durango, *B15512*.
**Decachaeta incompta* (DC.) K. & R.	16	MEXICO. CHIAPAS: Ixtapa, *B14062*.
Eupatoriadelphus maculatus (L.) K. & R.	10	UNITED STATES. NEW HAMPSHIRE: Chesire Co., *Gregory 495*.
Eupatoriadelphus maculatus	10	UNITED STATES. MICHIGAN: St. Joseph Co., *R20512*.
Eupatoriadelphus purpureus (L.) K. & R.	10	UNITED STATES. TENNESSEE: Van Buren Co., *R20443*.
Eupatoriadelphus purpureus	10	UNITED STATES. NORTH CAROLINA: McDowell Co., *R20474*.
Eupatorium hyssopifolium L. var. *hyssopifolium*	20	UNITED STATES. TENNESSEE: Monroe Co., *R20486*.
Eupatorium perfoliatum L.	10	UNITED STATES. MISSOURI: Wayne Co., *R20486*.
Eupatorium perfoliatum	10	UNITED STATES. TENNESSEE: Loudon Co., *R20491*.
Eupatorium rotundifolium L. var. *ovatum* (Bigel.) Torrey	20	UNITED STATES. TEXAS: Hardin Co., *R19433*.
Eupatorium rotundifolium var. *ovatum*	$2n$ = 39–40	UNITED STATES. NORTH CAROLINA: McDowell Co., *R20484*.
Eupatorium serotinum Michx.	10	UNITED STATES. TENNESSEE: Monroe Co., *R20484*.
Eupatorium serotinum	10	UNITED STATES. INDIANA: Monroe Co., *R20500*.
Eupatorium serotinum	10	UNITED STATES. MISSOURI: Francois Co., *R20532*.
Eupatorium serotinum	10	UNITED STATES. ARKANSAS: Saline Co., *R20564*.
**Fleischmannia capillipes* (Benth. ex Oerst.) K. & R.	ca. 10	MEXICO. CHIAPAS: Tapanatepec, *B13713*.
**Fleischmannia imitans* (B. L. Rob.) K. & R.	29	MEXICO. CHIAPAS: Mun. Chiapa del Corzo, *R19773*.
**Fleischmannia pastazae* (B. L. Rob.) K. & R.	20	ECUADOR. TUNGURAHUA: ca. 21 kms E of Baños, *K6553*.
Fleischmannia pastazae	20	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6556*.
**Fleischmannia plectranthifolia* (Benth. ex Oerst.) K. & R.	10	COSTA RICA. HEREDIA: ca. 15 kms N of Barba, *K6410*.
Fleischmannia pratensis (Klatt) K. & R.	20	MEXICO. CHIAPAS: Mun. Las Margaritas, *B9134*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Fleischmannia pratensis	20	MEXICO. CHIAPAS: Ocozocuatla de Espinosa, *B10326*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: 11 kms E of Pacayas, *K6540*.
Fleischmannia pratensis	ca. 20	ECUADOR. TUNGURAHUA: ca. 7 kms E of Baños, *K6540*.
Fleischmannia pratensis	20	COSTA RICA. SAN JOSÉ: La Palma, *K6737*.
Fleischmannia pratensis	ca. 20	COSTA RICA. SAN JOSÉ: ca. 16 kms W of Santa Ana, *K6747*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: El Muñeco, *K6767*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: El Muñeco, *K6768*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: Navarro, *K6772*.
Fleischmannia pratensis	ca. 20	COSTA RICA. CARTAGO: 2 kms SW of Tapantí, *K6775*.
Fleischmannia pratensis	20	COSTA RICA. SAN JOSÉ: ca. 8 kms N of Nubes, *K6780*.
Fleischmannia pratensis	20	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito, *K6802*.
Fleischmannia pratensis	20	COSTA RICA. HEREDIA: ca. 9 kms N of Barba, *K6809*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: 1 km NE of Santa Rosa, *K6813*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: ca. 6 kms NE of San Rafael de Irazú, *K6827*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: ca. 8 kms W of Tucurrique, *K6845*.
Fleischmannia pycnocephala (Less.) K. & R.	30	MEXICO. CHIAPAS: Mun. La Trinitaria, *B8389*.
Fleischmannia pycnocephala	30	GUATEMALA. Mun. San Mateo Ixtatán, *B8674*.
Fleischmannia aff. *pycnocephala*	20	MEXICO. CHIAPAS: Teopisca, *B13079*.
Fleischmannia pycnocephala	20	MEXICO. OAXACA: El Tejocote, *K6451*.
Fleischmannia pycnocephala	20	MEXICO. VERACRUZ: 7 kms SW of Coscomatepec, *K6488*.
Fleischmannia pycnocephala	ca. 40	GUATEMALA. ALTA VERAPAZ: 5 kms NE of San Pedro Carchá, *K7125*.
Fleischmannia pycnocephala	42–44 + $2\text{–}4_{I}$	GUATEMALA. BAJA VERAPAZ: ca. 53 kms SE Cobán, *K7128*.
**Fleischmannia pycnocephaloides* (B. L. Rob.) K. & R.	30	GUATEMALA. HUEHUETENANGO: San Juan Ixcoy, *B8468*.
**Fleischmannia seleriana* (B. L. Rob.) K. & R.	10	MEXICO. VERACRUZ: 3 kms W of Ciudad Mendoza, *K6485*.
Fleischmannia sp.	12 + $1\text{–}3_{I}$ (rarely 13 looking or 11 + 3_{I})	GUATEMALA. SACATEPEQUEZ: Ciudad Vieja, *K7078*.
Fleischmannia sp.	10	GUATEMALA. ALTA VERAPAZ: San Cristóbal Verapaz, *K7110*.
**Guevaria alvaroi* K. & R.	10	ECUADOR. AZUAY: ca. 11 kms NE of Girón, *K6673*.
**Guevaria sodiroi* (Hieron. ex Sod.) K. & R.	10	ECUADOR. CAÑAR: ca. 13 kms NW of Azogues, *K6615*.
Guevaria sodiroi	10	ECUADOR. CAÑAR: ca. 14 kms NW of Azogues, *K6617*.

TABLE 1. (Continued).

Species	n	Locality and collection number
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, *K6655*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 19 kms W of Cuenca, *K6664*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 6 kms SE of Cumbe, *K6698*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 7 kms SE of Cumbe, *K6706*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 13 kms S of Cumbe, *K6714*.
Guevaria sodiroi	10	ECUADOR. CAÑAR: 20 kms NW of Azogues, *K6882*.
Guevaria sodiroi	10	ECUADOR. AZUAY: 39 kms S of Cumbe, *K6904*.
**Hebeclinium bullatissimum* (B. L. Rob.) K. & R.	10	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6557*.
Hebeclinium bullatissimum	10	ECUADOR. TUNGURAHUA: ca. 26 kms N of Puyo, *K6571*.
Hebeclinium macrophyllum (L.) DC.	10	MEXICO. CHIAPAS: Ocozocuatla, *B13580*.
Hebeclinium macrophyllum	10	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6868*.
**Heterocondylus vitalbae* (DC.) K. & R.	ca. 20	COSTA RICA. CARTAGO: Navarro, *K6774*.
Hofmeisteria fasciculata (Benth.) Walp.	18	MEXICO. BAJA CALIFORNIA: Bahía de la Concepción, *Wiggins 19000*.
Isocarpha atripicifolia (L.) R. Brown	10	GUATEMALA. ZACAPA: ca. 4 kms NNW of Zacapa, *K7376*.
Isocarpha oppositifolia (L.) R. Brown	10	MEXICO. YUCATAN: Chichén Itzá, *K6859*.
**Koanophyllon hylonomum* (B. L. Rob.) K. & R.	10	COSTA RICA. ALAJUELA: 12 kms N of Quesada, *K6432*.
**Koanophyllon ravenii* K. & R.	ca. 10	MEXICO. CHIAPAS: Chiapa del Corzo, *B13472*.
Malperia tenuis S. Watson	10	MEXICO. BAJA CALIFORNIA: 2.7 mi W of San Felipe, *R14764* (DS).
**Matudina corvii* (McVaugh) K. & R.	16	MEXICO. CHIAPAS: Chiapa de Corzo, *B13473*.
Mikania micrantha H.B.K.	17	ECUADOR. TUNGURAHUA: ca. 11 kms E of Baños, *K6544*.
Mikania micrantha	ca. 19	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6870*.
Mikania micrantha	19	ECUADOR. CAÑAR: 23 kms ESE of El Triunfo, *K6999*.
**Mikania scandens* (L.) Willd.	ca. 19	UNITED STATES. DELAWARE: Sussex Co., *K6847*, *K6848*.
**Mikania vitifolia* DC.	ca. 20	ECUADOR. CAÑAR: 26 kms ESE of El Triunfo, *K7001*.
**Neomirandea allenii* K. & R.	17–20	PANAMA. COCLÉ: La Mesa, *Croat 37430*.
Neomirandea angularis (B. L. Rob.) K. & R.	ca. 24	COSTA RICA. CARTAGO: 20 kms SE of Orosi, *K6419*.
Neomirandea angularis	ca. 20	COSTA RICA. SAN JOSÉ: La Palma, *K6422*.
**Neomirandea biflora* K. & R.	ca. 25	COSTA RICA. CARTAGO: ca. 9 kms NE of San Rafael de Irazú, *K6835*.
**Neomirandea burgeri* K. & R.	20	COSTA RICA. SAN JOSÉ: Cerro de la Muerte, *K6413*.
Neomirandea costaricensis K. & R.	17	COSTA RICA. SAN JOSÉ: ca. 17 kms SE of Empalme, *K6760*.
Neomirandea costaricensis	ca. 17	COSTA RICA. SAN JOSÉ: ca. 8 km SE of Empalme, *K6764*.

TABLE 1. (Continued).

Species	n	Locality and collection number
Neomirandea costaricensis	17	COSTA RICA. SAN JOSÉ: ca. 9 kms SE of Cañon, *K6791*.
Neomirandea costaricensis	17_{II} + 1 B chromosome	COSTA RICA. HEREDIA: ca. 10 kms N of San Rafael, *K6796*.
Neomirandea costaricensis	17	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito, *K6801*, *K6804*.
**Neomirandea eximia* (B. L. Rob.) K. & R.	17	COSTA RICA. SAN JOSÉ: La Palma, *K6738*, *K6739*, *K6742*.
Neomirandea eximia	ca. 17	COSTA RICA. SAN JOSÉ: ca. 25 kms S of Cartago, *K6756*.
Neomirandea eximia	17 + 4– 5 supernumerary chromosomes	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito *K6803*.
**Oxylobus oaxacanus* Blake	16	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9587*.
**Peteravenia phoenicolepis* (B. L. Rob.) K. & R.	10	MEXICO. CHIAPAS: Mun. Chamula, *B7315*.
Peteravenia phoenicolepis	10	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8289*.
Peteravenia phoenicolepis	ca. 17	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B14148*.
**Phalacraea ecuadorensis* K. & R.	20	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, *K6653*.
Piqueria trinervia Cav.	11	MEXICO. CHIAPAS: Mun. La Trinitaria, *B8390*.
Piqueria trinervia	11	MEXICO. CHIAPAS: Teopisca, *B13086*.
Piqueria trinervia	ca. 24	COSTA RICA. CARTAGO: Volcán Irazú, *K6438*.
Piqueria trinervia	ca. 22 + 1–2 frags.	COSTA RICA. CARTAGO: ca. 3 kms NE of Cot, *K6812*.
Pleurocoronis pluriseta (A. Gray) K. & R.	9	UNITED STATES. CALIFORNIA: Riverside Co., *R11465*.
Pleurocoronis pluriseta	9	MEXICO. SONORA: Punta Peñasco, *R11665*.
Polyanthina nemorosa (Klatt) K. & R.	10 (2 larger bivalents)	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6559*.
**Sclerolepis uniflora* (T. Walter) Porter	15	UNITED STATES. NEW JERSEY: Cape May Co., *K7150* (part).
Sclerolepis uniflora	ca. 30	UNITED STATES. NEW JERSEY: Cape May Co., *K7150* (part).
Stevia berlandieri A. Gray	12	MEXICO. DURANGO: El Palmito, *B14187*.
Stevia elatior H.B.K.	ca. 23	MEXICO. CHIAPAS: Mun. Chamula, *B7067*.
Stevia elatior	11	MEXICO. OAXACA: El Tejocote, *K6459*.
Stevia elatior	11	ECUADOR. LOJA: 2 kms E of Loja, *K6909*.
Stevia elatior	ca. 33_I	GUATEMALA. HUEHUETENANGO: 53 kms N of Quezaltenango, *K7048*.
Stevia elatior	ca. 33_I	GUATEMALA. TOTONICAPÁN: 31 kms S of Huehuetenango, *K7050*.
Stevia elatior	ca. 33_I	GUATEMALA. TOTONICAPÁN: 10 kms E of Totonicapán, *K7068*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Stevia lucida Lag.	12	MEXICO. CHIAPAS: San Cristóbal las Casas, *B7120.*
Stevia ovata Willd.	34_{I}	MEXICO. CHIAPAS: Teopisca, *B13070.*
Stevia ovata	ca. 60_{I}	MEXICO. CHIAPAS: Mun. Chamula, *B13737.*
Stevia ovata	$32–34_{I}$	MEXICO. CHIAPAS: Ixtapa, *B14061.*
Stevia ovata	36_{I}	MEXICO. CHIAPAS: San Cristóbal las Casas, *B14153.*
Stevia ovata	36_{I}	GUATEMALA. ALTA VERAPAZ: 4 kms W of San Cristóbal Verapaz, *K7111.*
Stevia polycephala Bertol.	12	MEXICO. CHIAPAS: Mun. Zinacantán, *B7995.*
Stevia polycephala	12	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8302.*
Stevia polycephala	12	GUATEMALA. HUEHUETENANGO: Mun. San Juan Ixcoy, *B8495.*
Stevia polycephala	12	GUATEMALA. SAN MARCOS: 5 kms SE of Palestina, *K7031.*
Stevia polycephala	12	GUATEMALA. SAN MARCOS: 20 kms NE of San Marcos, *K7040.*
Stevia polycephala	12	GUATEMALA. TOTONICAPÁN: 12 kms SE of San Cristóbal Totonicapán, *K7054.*
Stevia serrata Cav.	ca. 27	MEXICO. CHIAPAS: Mun. Chamula, *B6650.*
Stevia serrata	ca. 33_{I}	GUATEMALA. TOTONICAPÁN: 21 kms NE of Quezaltenango, *K7042.*
Stevia serrata	ca. 54_{I}	GUATEMALA. TOTONICAPÁN: 24 kms NE of Quezaltenango, *K7043.*
Stevia subpubescens Lag.	12	MEXICO. SINALOA: El Palmito, *B14184.*
Stevia subpubescens	ca. 12	MEXICO. MORELOS: Tres Cumbres, *B14229.*
**Stevia tephrophylla* Blake	12	MEXICO. CHIAPAS: Ocozocuatla, *B13643.*
Stevia tephrophylla	ca. 12	MEXICO. CHIAPAS: Ocozocuatla, *B10346.*
Stevia trifida Lag.	11	MEXICO. SINALOA: Concordia, *B1647.*

* First chromosome number report for this species.

been reported for one species of *Adenostemma*, and $n = 8$ has been suggested, probably erroneously, for species of *Isocarpha* and *Ayapana*. It is probable that no other tribe in the family, except the Cynareae and Mutisieae, has as few species with low chromosome numbers.

Differences in chromosome size and shape have been mentioned in the studies of Grant (1953) and Gaiser (1953, 1954). While dealing with *Eupatorium* s. lat. in eastern North America, Grant reported two size ranges of chromosomes. For species now treated as *Eupatorium* s. str. and *Eupatoriadelphus*, with $n = 10$, the size ranged from 2.5–6.5 μm in length. For the group now recognized as *Ageratina*, with $n = 17$, the size ranged between 1.5–3.0 μm. One species now recognized as a *Conoclinium* has $n = 10$, as in the former group, but the chromosomes fall within the size range of the latter group. Grant treated these three groups as cytologically distinct.

Gaiser (1954) compared the taxa then placed in the subtribe Kuhniinae. This subtribe has since been shown to be artificial, so that Gaiser's comparison was between three groups that we do not now consider closely related. *Carphochaete* was distinguished as a small shrub without basal rosettes having a squamiform pappus and a gametic chromosome number of $n = 11$. The genus had the highest chromosome number and greatest content of chromatin per complement; it also had 3 pairs of isobrachial short chromosomes. The genera *Garberia*, *Carphephorus*, *Liatris*, and *Trilisa* (including *Latrisa*) were distinguished by alternate leaves forming basal rosettes in younger plants, a plumose or capillary pappus, and a gametic chromosome number of $n = 10$. *Garberia* was distinct among these in being a shrub and in having one of the two short pairs of chromosomes heterobrachial. The third group of genera, including *Brickellia*, *Kuhnia* and *Barroetia*, had leaves alternate to opposite, plants shrubby to annual without basal rosettes, pappus capillary to plumose, and a gametic chromosome number of $n = 9$. *Barroetia* and *Kuhnia* both had only medium and short chromosomes. *Brickellia* (Gaiser, 1953) had chromosomes of some species as in *Kuhnia* and *Barroetia*, but in most species the complements included longer chromosomes.

Gaiser (1953, 1954) noted the variation in karyotype in the *Brickellia* series and correlated this with variation in habit of the plants. Karyotypes including some long chromosomes were characteristic of shrubby plants. Karyotypes with only medium or short chromosomes occurred in more herbaceous plants. An apparent trend toward reduced DNA content in weedy species (Bennett, 1972) is also illustrated in the tribe in the genus *Fleischmannia*, in which a weedy annual species has a gametic chromosome number of $n = 4$, with most other species being perennial and having $n = 10$ and multiples of 10.

Pollen and Cell Size Correlation

Gaiser (1950b) made observations on morphological characters in relation to polyploidy in *Liatris* series *Punctatae*. Overall size showed no reliable correlation with chromosome number though corollas, styles, pappus, and inner phyllaries tended to be slightly longer in tetraploids than in diploids. The strongest correlation was in cell size. Tetraploid pollen and guard cells were larger than in diploids and the hexaploids showed a correspondingly larger size than the tetraploids. Another possible size correlation with polyploidy is seen in the two closely related genera *Phalacraea* and *Guevaria*. The former is larger in most parts and has pollen grains ca. 25 μm in diameter. The single chromosome count shows $n = 20$. *Guevaria* is a genus of distinctly smaller plants with pollen grains nearer 20 μm in diameter and chromosome counts of $n = 10$. Variations of pollen size and chromosome number are not notably correlated in other members of the tribe.

Other modifications of pollen are associated with meiotic irregularities. Holmgren (1919) studied the modified development and defective pollen formation in *Eupatorium glandulosum* (= *Ageratina adenophora*), an apomictic species with $2n = 51$. Holmgren recognized the species as a triploid related to *Eupatorium ageratoides* (= *Ageratina altissima*) and *Eupatorium* (*Ageratina*) *purpusii* having chromosome numbers of $n = 17$. *Ageratina riparia* is another weedy, widely adventive species of the genus with reports of $2n = 48$ correlated with defective pollen. Apomixis is common in *Ageratina* and the infrequency of normal sexual reproduction may be a major factor in the development of the more than 200 species. Pollen variation also occurs in other genera of the Eupatorieae but most notably in *Stevia* where as many as four distinct pollen states have been recognized in some species (King & Robinson, 1967). The most common modified state has altered furrow patterns and has a larger size than in normal grains. Grashoff (1972) related such pollen variations directly to irregularities in meiosis. In contrast to *Ageratina*, *Stevia* includes many sexually reproducing populations within its apomictic species, and natural hybridization is frequent between some species (Grashoff, 1972).

Chromosome Numbers and Phylogeny in the Eupatorieae

Previous subtribal concepts have been based primarily on the form of pappus, the ribbing of the achene, and the development of the anther appendage. The four subtribes must now be considered almost totally artificial and useless for phylogenetic comparisons. Traditionally, Ageratinae has included those genera not placed in one of the other subtribes. Piqueriinae contained most but not all of the genera with reduced anther appendages, including *Phania* which is most closely related to *Ageratum*, *Ophryosporus* which is closer to *Critonia*, and *Podophania* which is a *Hofmeisteria*. *Piqueria* itself contained elements belonging to three remotely related groups, *Koanophyllon*, *Ophryosporus*, and *Erythradenia*. The subtribe Kuhniinae, with more numerous ribs on the achenes, contained elements related to *Brickellia* with chromosome complements of $n = 9$; *Liatris*, with mostly $x = 10$; *Carphochaete*, which is more closely related to *Stevia*, with $x = 11$; and *Kanimia*, which is related to *Mikania* with $x =$ mostly 17–20. These genera differ greatly in many morphological characters as well as their cytology. Adenostemmatinae was the smallest subtribe and, with the exclusion of *Hartwrightia*, the only natural one (King & Robinson, 1974a).

Although the previous subtribal concepts are rejected, no new concepts have yet been formalized. Actually, it is at precisely this level of relationships that cytology might prove most helpful and at least some of the evolutionary trends are reflected by cytology. It seems best for the purposes of this study to discuss the Eupatorieae in terms of cytological groups, starting with the most diverse elements having $x = 10$ and proceeding through the less numerous groups with $x = 4$, 5, and 9. The treatment concludes with the genera having chromosome numbers higher than $x = 10$, including two major groups with $x = 11$–12 and with $x = 16$–18. See Table 2.

GENERA WITH $X = 10$

Included here is one of the largest complexes in the tribe, having members concentrated in the eastern parts of both North and South America. The members tend to have papillose style branches and corolla lobes, anther collars with strong annulate thickenings, and the pappus setae often with rounded apical cells. In the group is *Eupatorium*, with the related *Eupatoriadelphus*, *Austroeupatorium, Stomatanthes* and *Hatschbachiella* (Group II), all of which have pubescent style bases; *Disynaphia*, with the related *Symphyopappus*, *Raulinoreitzia*, *Grazielia* and *Campovassouria* (Group III), all having plain style bases, subimbricate phyllaries, and 5 flowers per head (King & Robinson, 1971d); and the vast group related to *Conoclinium* and *Gyptis*, including *Agrianthus*, *Barrosoa*, *Campuloclinium*, *Conocliniopsis*, *Dasycondylus*, *Lourteigia*, *Neocuatrecasia*, *Tamaulipa*, *Trichogonia*, *Trichogoniopsis*, and *Urolepis* (Group IV) having usually plain style bases, mostly eximbricate phyllaries, and more than 5 flowers per head. The first group in the complex is noteworthy within the tribe for its natural occurrence in the eastern hemisphere, *Eupatorium* reaching Asia and Europe in the north and *Stomatanthes* having 3 species across the Atlantic in Africa. The group including *Gyptis* is notable for its extreme elaboration and predominance in easternmost Brazil. The entire complex, with few exceptions, includes only species with gametic chromosome numbers of $n = 10$ or multiples of 10. About 10 species of *Eupatorium* s. str. from North America and Asia have plants with $n = 15$ in addition to the apparently more common ones of $n = 10$ and $n = 20$. Such numbers supposedly result from hybridization between the different ploidy levels that are common in the genus, and are perpetuated by apomixis. Grant (1953) noticed the small size of the chromosomes of *Conoclinium coelestinum* (L.) DC., but related forms have not been studied for this characteristic.

Ageratum and *Phania* seem related to *Gyptis* but have been separated here into a series of more western genera (Group VI) with reduced pappus. These are morphologically transitional to genera having gametic chromosome numbers of $n = 11$ or 12.

Another major element in the Eupatorieae having $n = 10$ is the assemblage of genera related to *Critonia* (Group XII), with genera such as *Koanophyllon*, *Fleischmanniopsis*, and *Eupatoriastrum* being concentrated in the more tropical parts of Central America, the West Indies, and northern South America. The genera *Austrocritonia* and *Neocabreria* are rather isolated members of this more typical series in southern Brazil, and there is a related complex in the Andes containing *Aristeguietia*, *Asplundianthus*, *Critoniella*, *Cronquistianthus*, and *Ophryosporus*. Members of the complex have phyllaries subimbricate to imbricate, but the group is most notable for its lack of specializations, being difficult to delimit and perhaps in part artificial. The group of genera including *Critonia* may be related to other genera with a gametic chromosome number of $n = 16$–18 through such genera as *Hebeclinium* which has $n = 10$.

More structurally distinct from *Critonia* but evidently closely related is the *Praxelis* group (XIII), occurring mainly in Brazil. In addition to *Praxelis* the group includes *Praxeliopsis, Lomatozoma, Eupatoriopsis, Eitenia* and the large genus *Chromolaena*, all having involucres that shed all their phyllaries at maturity. *Chromolaena* has a range extending to Mexico and the West Indies where the subgenus *Osmiella* seems to intergrade with some members of the *Critonia* group in the area. *Osmiopsis plumeri* (Urban & Ekman) K. & R. of Haiti has a mixture of *Chromolaena* and *Koanophyllon* floral features not explicable by simple convergent evolution. In spite of marked involucre, corolla, and anther differences, *Chromolaena* of the *Praxelis* group and *Koanophyllon* of the *Critonia* group seem to have retained sufficient cytological similarity to be able to form successful hybrids.

The distinctive group of genera related to *Ayapana* (Group VIII) is largely restricted to South America with a few widely distributed or adventive species. The group is most inadequately represented in cytological studies. The genera *Ayapanopsis, Gongrostylus, Gymnocondylus, Alomiella*, and *Monogerion* have not been counted. Within *Ayapana* itself $n = 17$ has been reported for one species, $n = 8$ and $n = 18$ for another, and a third species is reported here with two counts of $n = 10$. The monotypic *Polyanthina* has been counted once as $n = 12 \pm 1$ and twice as $n = 10$; *Isocarpha* earlier reported as having a gametic chromosome number of $n =$ ca. 8, is now known to have $n = 10$; *Heterocondylus* is reported here as $n =$ ca. 20; and *Condylidium*, which is perhaps more distantly related to the other genera in the series, has $n = 10$. One is inclined even on the basis of this small sample to suggest a base number of $x = 10$ for the group, although the situation in *Ayapana* itself, with about a dozen species, should be clarified. Certainly, other characters show the group has no close relationship with others having chromosome numbers $n = 11$, 12, 17 or 18.

Liatris and the related genera, *Carphophorus, Garberia, Litrisa*, and *Trilisa* of the southeastern United States (Group X) have a basic chromosome number of $x = 10$, with polyploidy only in *Liatris*. Among the diploid series of *Liatris* (Gaiser, 1949, 1950a, 1950b), Spicatae and Pycnostachyae exhibited variation in chromosome length, with some medium and long chromosomes with subterminal constrictions, whereas Graminifoliae and Pauciflorae have more uniform karyotypes. Polyploidy occurs in series Punctatae and has been important in the evolution of species in this group.

GENERA WITH $N = 4$

The genus *Fleischmannia* (Group XI) has many features of the *Gyptis* relationship but differs by several important details including the usually subimbricate involucre and the unique form of papillae on the corolla. Similarity of habit has caused confusion with some species of *Ageratina*, but the latter genus is strikingly distinct in floral anatomy and cytology (King & Robinson, 1970a, 1970b). Most specimens of *Fleischmannia* that have been counted have $n = 10$ or mul-

TABLE 2. General distribution, habit, and chromosome number of genera of Eupatorieae.

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
		I. Adenostemmatinae				
Adenostemma	pantropical	P	20	4	10, 5	
		II. Eupatoriinae				
Eupatorium	e. U.S., Asia, Eur.	P	38	20	10, 15, 20	yes
Eupatoriadelphus	e. North Amer.	P	4	4	10, 20	yes
Austroeupatorium	S. Amer., advent.	P,S?	11	2	10	
Stomatanthes	Brazil, Africa	P	15	1	10	
		III. Disynaphia Group				
Campovassouria	s. Brazil, Parag., Urug., n. Argent.	P	1	1	10	
Disynaphia	Brazil, Uruguay	P	12	1	10	
Grazielia	Brazil	P	9	1	10	
Raulinoreitzia	Brazil	P	2	1	10	
Symphyopappus	Brazil	P	13	2	10	
		IV. Gyptis Group				
Barrosoa	S. America	P	11	1	10	
Campuloclinium	Cent. Amer. to Brazil	P	20	1	10	
Conocliniopsis	S. America	P	1	1	10, 30	yes
Conoclinium	U.S., Mexico	P	3	3	10	
Gyptis	Brazil	P	7	1	30	
Lourteigia	Colombia, Venezuela	P	7	2	10	
Tamaulipa	Texas, n. Mexico	P	1	1	10	
Trichogoniopsis	Brazil	P	2	1	10	
Vittetia	Brazil	P	1	1	10	
		V. Acritopappus Group				
Acritopappus	Brazil	S	3	1	9	
		VI. Piqueria Group				
Ageratum	trop. Amer., advent.	P	43	14	10, 15, 20	yes
Ascidiogyne	Peru	P	1	1	10	

TABLE 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
Carphochaete	sw. U.S., Mexico	S	5	2	11	
Cronquistia	Mexico	P	1	1	12	
Guevaria	Ecuador, Peru	P,sS	4	2	10	
Microspermum	Mexico	P	7	3	12	
Phalacraea	Colombia to Peru	P	5	1	20	
Piqueria	Mex., C. Amer., W. Ind.	P	7	2	12, 25	yes
Stevia	Mex., C. Amer., S. Amer.	A,P,S	150–200	37	11, 12, ca. 30 $2n = 24, 33, 34, 36,$ ca. 43, 46, 40–47 var, $2–8_{II} + 30–18_{I}$	yes
		VII. Trichocoronis Group				
Trichocoronis	Texas, Mexico	P	2	1	15	
Sclerolepis	e. U.S.	P	1	1	15	
Shinnersia	Texas, Mexico	P?	1	1	ca. 30	
		VIII. Ayapana Group				
Ayapana	W. Ind., S. Amer., advent.	P	11	3	8, 10, 17, 18	yes
Condylidium	C. Amer., W. Ind., n. S. Amer.	P	2	1	10	
Heterocondylus	C. Amer., S. Amer.	P,S	12	1	ca. 20	
Isocarpha	trop. Amer.	P	12	2	10	
Polyanthina	Costa Rica, n. S. Amer.	P	1	1	10, (12 ± 1?)	
		IX. Alomiinae				
Barroetia	Mexico	P	6	3	9	
Brickellia	mostly sw. U.S., Mex., Central America	A,P,S	100	51	9	
Brickelliastrum	sw. U.S.	P	1	1	10	
Carminatia	Mexico	P	2	1	10	
Crossothamnus	Peru	S	1	1	10	
Malperia	sw. U.S., Mexico	P	1	1	10	
Phanerostylus	n. Mexico	sS	3	1	9	
Pleurocoronis	sw. U.S., w. Mexico	sS	3	2	9	

Table 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
		X. Liatris Group				
Carphephorus	se. U.S.	P	5	4	10	
Garberia	Florida	S	1	1	10	
Liatris	se. U.S.	P	34	20	10, 20, 30	yes
Litrisa	se. U.S.	P	1	1	10	
Trilisa	se. U.S.	P	2	2	10	
		XI. Fleischmannia Group				
Fleischmannia	N. Amer., w. S. Amer. advent.	A,P	75	10	10, 4, 20, 29, 30	yes
		XII. Critonia Group				
Aristeguietia	Andes	S	20	4	10	
Asplundianthus	n. S. Amer.	S	9	1	10	
Austrocritonia	Brazil	S	3	1	10	
Critonia	C. Amer., W. Ind., n. S. Amer.	P,S,T	33	4	10	
Critoniella	Colombia, Venezuela	P	5	1	10	
Koanophyllon	trop. Amer.	P,S	109	5	10, 20	yes
Ophryosporus	S. Amer.	P,S	38	1	10	
		XIII. Praxelis Group				
Chromolaena	trop. Amer., advent.	P,S	over 130	11	10, 29	yes
Praxelis	S. Amer.	P	13	1	$2n = 48, 51$, ca. 80 $20\ (7_{II} + 26_{I})$	
		XIV. Hebeclinium Group				
Bartlettina	trop. N. & S. Amer.	P,S	20	5	10, 16	
Decachaeta	Mex., Cent. Amer.	S	7	1	16	
Hebeclinium	mostly S. Amer., 1 trop. Amer.	P,S	18	4	10	

TABLE 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
Matudina	s. Mexico	P,S	1	1	16	
Peteravenia	Mex., Cent. Amer.	P,S	4	1	10, ca. 17?	?
XV. Neomirandea Group						
Neomirandea	Mex., C. Amer., n. S. Amer.	S	24	5	17, 20, ca. 24, 25	
XVI. Mikania Group						
Mikania	trop. Amer., Africa, trop. Asia	P,Li,S	300	13	ca. 16, 17, 18, 19, 20, $2n = 34$–38	
XVII. Ageratina Group						
Ageratina	N. & C. Amer., W. Ind., w. S. Amer., advent.	P,S	230	38	ca. 16, 17, 18, 20, ca. 25, ca. 40, ca. 42, 48, $2n = 48$, 50, 51, 55–2 frag., 68–69, ca. 80, ca. 85	yes
Oxylobus	Mex., n. S. Amer.	S	5	4	16	
XVIII. Hofmeisteria Group						
Hofmeisteria	Mexico	P,S	8	1	18, 19	

tiples of that number. Various authors including Turner & King (1964) and Baker (1967) have reported $n = 4$ in two annual species of the genus, *F. sinclairii* and *F. microstemon*. Baker regards the lower number as derived and states: "This is suggested by the fact that the chromosomes of the four-paired cytotype are much larger than those of the ten-paired form and by the behavior of the hybrid between them (with $2n = 14$). At the first meiotic division of the pollen mother cells in this hybrid the commonest configuration to be seen is of four multivalents (or at least bivalents) involving the four large chromosomes of the four-paired cytotype, together with an appropriate number of univalents. This is consistent with an evolution of the four-paired condition by gradual reduction of the chromosome number by unequal translocations followed by loss of centromeres on the classic *Crepis* model (Tobgy, 1943). The asymmetry of the chromosomes in the four-paired plants is also in keeping with this ancestry." Recent revisions have shown that all specimens with $n = 4$ were *F. microstemon* and that *F. sinclairii*, which has $n = 10$ exclusively is not so closely related, having differences in leaf texture, size of heads, shape and pubescence of phyllaries, and in the form and color of the achenes. More recently, Grashoff et al. (1972) have reported $n = 4$ from *F. hymenophyllum*, a large probably perennial herb from Costa Rica and Panama that shows no particular relationship to *F. microstemon*. In spite of the lower numbers in two species, the original basic chromosome number of *Fleischmannia* seems to have been $n = 10$.

Recent reidentifications have also provided a revised concept for *Fleischmannia pycnocephala*, which is now seen to include only plants with $n = 20$, $n = 30$ and variants in Guatemala reported in this study as $n =$ ca. 40 and $n = 42$–44 with 2–4_I. Many previous reports belong to related species, especially *F. pratensis* which has $n = 20$. The resegregated *F. sonorae* (A. Gray) K. & R. of Sonora and Arizona resembles *F. incarnata* (Walter) K. & R. of the eastern United States and *F. seleriana* (B. L. Robinson) K. & R. of the eastern escarpment of Chiapas and Veracruz in having $n = 10$.

GENERA WITH $N = 5$

This low count has been reported once by Turner & Irwin (1960, as *Adenostemma brasiliense*) for a specimen now determined as *Adenostemma involucratum* K. & R. Four other species including the true *A. brasiliense* (Pers.) Cass. and *A. platyphyllum* Cass. (once as *A. lavenia*) are reported as $n = 10$. Turner and Irwin have suggested that $n = 5$ is the basic chromosome number for the genus, but in context, reduction from $n = 10$ in this single species appears more probable. The closely related genera *Sciadocephala* and *Gymnocoronis* have not been counted. The subtribe Adenostemmatinae (Group I) is one of the most distinctive elements of the Eupatorieae but the characteristic viscid knobs of the achenes and unsclerified interstices of the receptacle indicate a specialized rather than primitive position in the tribe.

GENERA WITH $X = 9$

The primary group of Eupatorian genera having chromosome counts of $n = 9$ has been studied extensively by Gaiser (1953, 1954) who studied 41 species of

Brickellia, 4 of *Kuhnia*, and 2 of *Barroetia* (Group IX). *Brickellia* has long been recognized as distinct, but exact limits have been so uncertain that Correll & Johnston (1970) have suggested possible reduction of the genus and *Mikania* to synonymy under *Eupatorium*. Harcombe & Beaman (1967), in a different approach, have abandoned the morphological characters and have delimited the genus on the basis of the distinctive $n = 9$ chromosome number. In reality, the *Brickellia* group is much more extensive than previously realized, being characterized by the usually very long and clavate style branches and a usually narrow corolla opening. The group includes genera such as *Helogyne*, *Leptoclinium*, and *Dissothrix* of South America, as well as many distinctive segregates previously placed in *Brickellia* or *Eupatorium*. Many of the genera, including *Asanthus*, *Flyiella*, *Alomia*, *Dyscritogyne*, *Kyrsteniopsis*, and *Steviopsis* of Mexico are not known cytologically. Among the genera that have been studied, the gametic chromosome number $n = 9$ has been characteristic of *Brickellia* (including *Kuhnia*), *Barroetia*, *Phanerostylis*, and *Pleurocoronis*. The number has not been reported yet for any of their strictly South American relatives. The gametic chromosome number n = 10 has been reported, however, from a number of related genera including *Malperia* (Raven in King, 1967a), *Brickelliastrum* (Watson, 1973, as *Brickellia*), and *Carminatia* of North America, as well as *Crossothamnus* (Turner et al., 1967, as *Eupatorium weberbaueri*) and *Austrobrickellia* (Krapovickas, 1951, as *Eupatorium patens*) from South America. The distribution of numbers suggests a derivation of $n = 9$ from the more characteristic Eupatorian $n = 10$ within the *Brickellia* group.

Two counts of $n = 9$ are available for the genus *Acritopappus* (Group V) [Coleman, 1970, as *Alomia longifolia* (Gardn.) B. L. Robinson]. Interpretation is difficult because relationships of the genus are not clear. There is some resemblance to the as yet uncounted *Radlkoferotoma* and there may be some relation to the *Gyptis* group in spite of the subimbricate phyllaries. *Acritopappus* is definitely not closely related to other members of the tribe having $n = 9$, and we presume that the chromosome number of this genus has been derived independently from $n = 10$.

GENERA WITH $x = 11$ OR 12

The known genera having $n = 11$ or 12 appear to be part of a larger group having strongly papillose corolla lobes and annulate thickenings in the cells of the anther collars (Group VI). The group shows a strong tendency for pappus reduction with squamiform and coroniform types represented. These features and chromosomal evidence both suggest strongly that the genera are related to one another and have no direct relationship to those with gametic chromosome numbers of $n = 16–18$.

In the group of genera with a gametic chromosome number of $n = 11$ or 12, *Stevia* and *Carphochaete* seem closely related as suggested by Turner (1959). The single species of *Cronquistia*, reported here as having $n = 12$, was originally described as a *Stevia* and has more recently been associated with *Carphochaete* (Grashoff, unpublished). Each of the three genera has its own distinctive style structure, with *Carphochaete* ($n = 11$) especially remarkable, indicating that stylar morphology alone is not a reliable indication of relationship. *Stevia* has been extensively treated cytologically by Grashoff (Grashoff et al., 1972) with the conclusion that shrubby species all have a gametic chromosome number of $n = 12$; herbaceous species with laxly paniculate arrangement of capitula have $n = 11$ with no aneuploidy; and herbaceous species with compact-corymbose arrangements of capitula mostly have $2n = 34$ univalents with considerable aneuploidy. The great variation and widespread apomixis in *Stevia* allows for interpretation of $2n = 33$ and $2n = 34$ as triploid derivatives of $n = 11$. There is some tendency, however, to interpret the $2n = 34_{I}$ found in *Stevia* as a potential $n = 17$ partly because of the common occurrence of $n = 17$ elsewhere in the tribe. Grashoff reports *S. jorullensis* H.B.K. as having $2n = 17_{II}$ and 34_{I} and *S. plummerae* var. *durangensis* as having $2n =$ ca. 17_{II}, and he suggests that among the compact-corymbose herbaceous species the alternate leaved species "may have numbers based on 11, 12, or 17 within the same species," while "the opposite leaved species appear to be based on $x = 17$ alone." Nevertheless, Grashoff does report the opposite leaved species *S. origanoides* as having both 34 univalents and 43 ± 1 univalents and Keil & Stuessy (1975) have since reported *S. origanoides* as having $n = 11$ and another opposite-leaved species *S. plummerae* var. *durangensis* as having $n = 44_{I}$. Such evidence and the lack of a close relationship of *Stevia* to any of the genera with $n = 17$ indicates that the counts for the genus should be interpreted on the basis of the known $n = 11$ and $n = 12$ numbers that are common in the genus and in related genera. Such reports as the $2n = 17_{II}$ in *S. jorullensis* and $2n =$ ca. 17_{II} in *S. plummerae* var. *durangensis* could be interpreted as the result of preferential pairing, although more observations would be highly desirable. In any case, the three elements within *Stevia* definitely seem, on the basis of overwhelming morphological and anatomical evidence, to be closely related to one another.

Reexamination of the microstructure of the genus *Macvaughiella* shows that the genus is related to the *Stevia* group rather than to the *Ageratina* group where it was recently placed (King & Robinson, 1970b). There is only an unpublished chromosome count of $n =$ ca. 13 by R. C. Jackson for *M. mexicana* (Sch. Bip.) K. & R. (MEXICO. CHIAPAS: 7 mi N of Arriaga, *Cronquist & Sousa 10459*).

Piqueria s. str. has a base chromosome number of $x = 12$ (25) and shares with *Stevia* the characteristic reduced number of flowers, equal to the number of phyllaries. *Microspermum* also seems related and Rzedowski (1970) has reviewed the cytology of 3 species, all having $n = 12$. A number of genera in South America resemble *Piqueria* and seem to be related. Thus far, however, all chromosome counts for these genera have been on a base of $x = 10$; *Ascidiogyne*, $n = 10$, *Phalacraea*, $n = 20$, and *Guevaria*, $n = 10$. Some close relatives of *Guevaria* remain uncounted, including *Ellenbergia* and *Ferreyrella* of the Andes, *Piqueriella* of eastern Brazil, and *Piqueriopsis* of western Mexico. The counts of $n = 10$ might reflect phyletic ties with the structurally similar widely distributed genus *Ageratum*, and the latter shows significant features in common with the *Gyptis* group. *Ageratum* has been reviewed by Johnson (1971) and has a basic chromosome number of $x = 10$. *Ageratum micropappum* Baker is a questionable member in the genus which lacks the characteristic conical receptacle. The species has been counted as $n = 9$. [BRAZIL. BAHIA: *Coleman 501* (Coleman, unpublished)].

The pattern of distribution of chromosome numbers and the interpretation of the structural evidence indicate that $n = 11$ and $n = 12$ in the present group have been derived by aneuploid increase within the group from $n = 10$, which is common both in this assemblage of genera and in other parts of the tribe.

GENERA WITH $N = 15$

The number has been obtained from various species of *Eupatorium* and from one plant of *Ageratum*, in both, it is almost certainly the result of hybridization between the more common populations with $n = 10$ and $n = 20$, and it could persist as a result of asexual reproduction. Otherwise the number is known in the tribe from members of the *Trichocoronis* group (VII). A single count is available for one of the two species of the genus *Trichocoronis* of the southwestern U.S. and central Mexico. *Trichocoronis* seems to be related to the recent taxonomic segregate *Shinnersia*. The many structural differences in the latter might be correlated with its extreme aquatic nature. A count of $n =$ ca. 30 has been obtained for *Shinnersia* by Chambers (King & Robinson, 1970c). This number could be a multiple of either 10 or 15 and leaves the base number of the group still in doubt. *Sclerolepis* is reported here as $n = 15$ and ca. 30.

GENERA WITH $X = 16–18$

The genera of this complex are variable in many features and comprise a number of distinct elements. The complex shows some common trends, however, that seem to preclude close relation to the genera with $n = 11$ and $n = 12$, a comparatively homogeneous assemblage. The cells of the anther collars are nearly or completely without annular thickenings and the corolla lobes of all but the *Ageratina* group lack papillae. The pappus is present and capillary in all but *Oxylobus* and *Erythradenia*. One specialization of the pappus is the tendency for fragile and deciduous setae in members of both the *Hebeclinium* and *Ageratina* groups.

The most significant result of the new reports in this paper is the recognition and partial clarification of a group of related genera (Group XIV) with many Mexican and Central American species having a gametic chromosome number of $n = 16$. The present report of $n = 16$ is the first for *Decachaeta*, a genus previously noted as a close relative of *Bartlettina*. Four species of *Bartlettina* are also reported here with a gametic chromosome number of $n = 16$. One of the four species, *B. sordida*, has been reported previously as $2n = 20$ by Holmgren (1919, as *Eupatorium ianthinum*) but the Holmgren identification has not been confirmed. Also, one *Bartlettina* from South America has been reported as having $n = 10$ (Powell & Cuatrecasas, 1970, as *Critonia paezense*) but the South American members of the genus are aberrant in a number of other details and seem at least subgenerically distinct. The number reported here for *Matudina* seems to confirm its relationship to *Bartlettina* and *Decachaeta*. In the original description of the single species of *Matudina*, McVaugh (1972, as *Eupatorium corvi*) made comparison with species placed in *Eupatoriastrum* s. str., for which no chromosomal information is available. *Eupatoriastrum*, although superficially similar to *Matudina*, is closely related to *Koanophyllon* in the *Critonia* series in which there is a base of $x = 10$. A probable close relative of *Bartlettina* is *Peteravenia*. In the latter only one of the four species has been examined cytologically, with two populations from central Chiapas having $n = 10$, a third collection from the same general area having $n =$ ca. 17 (20?), suggesting a probable basic chromosome number of $x = 10$ for the genus. An undoubted relative of *Bartlettina* is the primarily South American genus *Hebeclinium* which is uniformly reported as having $n = 10$. The gametic chromosome number of $n = 16$ in *Decachaeta*, *Matudina*, and at least 4 of the approximately 20 species of *Bartlettina* could be most easily derived by aneuploid reduction from $n = 20$. It is probable but not certain that the $n = 16$ in the three genera was derived from a single common ancestor having that number.

The genus *Neomirandea* (Group XV) consists of two rather distinctive but related elements. The subgenus *Critoniopsis* is known by counts of $n = 17$. The subgenus *Neomirandea* has a variety of reports indicating $n = 20$ and $n = 25$. The occurrence of these numbers might be an indication of multiples of $x = 5$ which seem to occur in scattered and isolated places in the tribe, or might have originated as a result of hybridization between plants with $n = 20$ and a putative $n = 30$. The cytological groups correlate completely with the subgeneric classification based on style bases and to some extent on corolla pubescence. The present counts include 3 species of subgenus *Neomirandea* representing its two major variations and many specimens of 2 species of subgenus *Critoniopsis*. Studies of the anatomy have given the distinct impression that subgenus *Neomirandea* of this mostly epiphytic genus is the derived element, even though it contains those species noted as terrestrial on labels. Recent field work shows that the supposedly terrestrial species are all restricted to rich humus substrates and often possess distinctive prop-root systems. Within the context of the tribe, however, it would seem that $n = 20$ would be the original basic number in the genus and $n = 17$ would be derived.

Mikania (Group XVI) and the weak segregate *Kanimia* have counts of $n =$ 17, 18, and 19 with a few additional reports of $n =$ ca. 16 and $n =$ ca. 20. There are varied reports in a number of species, and it is uncertain how much is real variation or how much is the result of the staining difficulties often noted in attempts to count chromosomes in *Mikania*. The two counts of $n =$ ca. 19 reported here for *M. scandens* represent the first for this endemic eastern North American species. Previous counts reported under this name represent related species that are sometimes included under a broader concept.

The largest genus of the tribe may ultimately prove to be *Ageratina*, and it includes the majority of species of the tribe for which $n = 17$ has been reported. Such counts have been regularly obtained for members of the genus from both North and South America. There is apomixis in the genus and a few species are evidently polyploid. One, *A. aschenborniana* (Schauer) K. & R. seems to include at least two cytotypes respectively with $n = 17$ and $n = 20$. The recent report of $n = 10$ by Grashoff et al. (1972) is less explicable. The specimen at the University of Texas thus annotated has a different collection number from that reported in the publication and might be held suspect. A new report of $n =$ ca. 10 in this study suggests again, however, that some lower numbers occur in the species. Three species of the northern Andes, *A. exerto-venosa* (Klatt) K. & R., *A. pseudochilca* (Benth.) K. & R., and *A. tinifolia* (H.B.K.) K. & R., belong to a distinctive group that is restricted to that area. Reports of *A. tinifolia* by Powell & King (1969) and reports of the other two in this paper show consistently $n =$ ca. 40, $n =$ ca. 40 + B chromosomes, or $n =$ ca. 42. Such numbers are not easily derived from $n = 17$ but might reflect a more basic $n = 20$ for the group.

Ageratina is the largest of a group of closely related genera including *Oxylobus*, *Piptothrix*, *Jaliscoa*, and *Spaniopappus* (Group XVII). *Oxylobus*, which differs from *Ageratina* in only one significant structure, the pappus, is nevertheless consistently reported as having $n = 16$. The chromosome number thus seems to confirm the conclusions based on anatomical features that *Oxylobus* is related closely to *Ageratina* rather than to *Ageratum* with $x = 10$ or to *Stevia* with $x = 11$ and 12. Structure would also dictate that the *Bartlettina-Decachaeta* series with $n = 16$ is sufficiently distinct to indicate an independent origin for the number in that group.

The great differences among the species with mostly $n = 16$–18 does not preclude the possibility that one very large and complex natural group may be involved. The *Bartlettina* series is not very different in some of its basic structures from subgenus *Critoniopsis* of *Neomirandea*. *Neomirandea* in turn shares a tendency for epiphytism and large quadrate corolla cells with *Mikania*. *Neomirandea* might also prove to be linked with *Ageratina* through such intermediates as the poorly known and possibly extinct *Standleyanthus*. In the context of the tribe the chromosome numbers in these genera were probably derived by aneuploid reduction from $n = 20$ which is still represented sporadically in the group.

GENERA WITH $N = 18$ AND 19

Hofmeisteria forms a very distinct element in the tribe Eupatorieae (Group XVIII), and there is no basis for association with the group of genera which primarily have $n = 16$–18. *Hofmeisteria* seems most likely derived independently from ancestors having $n = 20$. Both $n = 18$ and $n = 19$ in *Hofmeisteria* are based upon reports from a single species, and further information would be highly desirable.

No likely ancestor is evident for *Hofmeisteria*, but its remote position recalls two other genera of a unique group, *Oaxacania* and *Carterothamnus*. It is these last two genera that possess the most primitive form of paleae in the tribe and which are most clearly in need of cytological investigation.

GENERAL SPECULATION ON NUMBERS

The overall distribution of chromosome numbers in the Eupatorieae indicates that the most likely original base number for the ancestor of the tribe was $n = 10$. Almost certainly reduction has occurred in *Fleischmannia* and *Adenostemma* to $n = 4$ and $n = 5$, respectively. Additional aneuploid reduction in chromosome number seems to have occurred in the ancestory of *Brickellia*, *Acritopappus*, and a few other genera with $n = 9$, and also in the derivation of genera with $n =$ 19, 18, 17, and 16. Plants with $n = 15$ seem to have been derived by hybridization between those with $n = 10$ and others with $n = 20$, in many cases followed by apomixis. The interpretation of $n = 25$ in *Neomirandea*, on the other hand, is more difficult. The possibility that some genera with $n = 19$, 18, 17, and 16 may have been derived from diploid parents with chromosome numbers lower than $n = 10$ cannot be excluded for all genera, but few such diploids are known, and none that are directly related to the plants with higher numbers.

In a single species of *Peteravenia*, both $n = 10$ and $n =$ ca. 17 are known, and, if the latter number can be confirmed, aneuploid reduction within the genus would be indicated. Four species of *Bartlettina* have $n = 16$, a fifth $n = 10$, and a similar relationship may be suspected for it. In any case, in the *Hebeclinium*-*Bartlettina* group the two numbers $n = 10$ and $n = 16$ seem well established in different members of a closely related group.

There seem to be no problems in the interpretation of a separate series in the *Piqueria*-*Stevia* relationship showing aneuploid gain from $n = 10$ to $n = 11$ and 12.

Recent studies of structural diversity, cytology, and phytogeography of the Eupatorieae have seemed to indicate a tribe much more diverse than previously published treatments would allow. The complexity of the new classification is considered a reflection of a complex phylogeny for the tribe, many parts of which seem to be very actively evolving.

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NOTE ADDED IN PROOF

Keil and Pinkava (1976) have recently reported a chromosome count of $n = 9$ for *Carminatia*, claimed glabrous style bases for two species of *Brickellia* s. str., and placed *Carminatia* in the synonymy of *Brickellia*. More recently Keil and Pinkava (1977) have corrected these errors and reported $n = 10$ for *Carminatia*.

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